

Breeding biology of Asian House Martin *Delichon dasypus* in a high-elevation area

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We present data on the breeding biology of the largest known colony of Asian House Martin *Delichon dasypus*, located in the Jiangxi Wuyishan Nature Reserve at 2,158 m in the Huanggang Mountains, China. Nest surveys conducted in abandoned buildings in a subalpine meadow during March–August 2007 and 2008 yielded 163 and 132 clutches, from 84 and 82 nests, respectively. Breeding pairs also laid multiple broods and replacement clutches. Average clutch size was 3.0 and 2.6 eggs for first and second broods respectively. Synchronous hatching was detected in 79% of clutches. The proportion of eggs hatching was 0.7 and 0.6 for first and second broods respectively, and the proportion fledging was 0.5 and 0.4 respectively. Nests situated inside buildings were more successful than those situated outside owing to greater protection from severe weather, which was the major cause of breeding failure. Nest losses caused by severe weather were more pronounced later in the breeding season.

INTRODUCTION

Many bird species raise only one brood per year because of a narrow period of suitable environmental conditions which prohibits multiple breeding attempts (Evans-Ogden & Stutchbury 1996). Others raise multiple broods per breeding season (Verhulst *et al.* 1997) and the total seasonal fecundity for these species depends on the number of breeding attempts (Geupel & DeSante 1990). One of the principal determinants of multiple broods is the duration of the breeding season, which is often directly related to the abundance and availability of food (Holmes *et al.* 1992, Morrison 1998).

At high elevations, climatic conditions are more severe and unpredictable, with greater daily variation (Lu 2005). Such variable weather may significantly increase the risk of nest failure and may influence parental investment in each clutch and offspring (Bulmer 1984). Consequently, bird species that occupy montane habitats may adjust their reproductive strategy by breeding over shorter periods and producing fewer broods or smaller-sized clutches than species at lower elevations (Sandercock *et al.* 2005, Bears *et al.* 2008).

We examined the reproductive ecology of the Asian House Martin *Delichon dasypus* in the high-elevation montane environment of the Huanggang Mountains in south-eastern China. This widespread migrant species is known to occupy a wide elevational gradient spanning both lowland and montane habitats from 800 to 3,000 m (Turner & Rose 1989). In the Huanggang Mountains, birds visit during March–August each year to breed at elevations above 2,000 m, where weather conditions are unpredictable, with severe rainstorms and typhoons. Our aim was to evaluate the reproductive biology and breeding success of this population under such environmental conditions.

METHODS

Study site

Fieldwork was conducted in the Jiangxi Wuyishan Nature Reserve, in the Huanggang Mountains (27°51'38"N 117°47'01"E), Jiangxi province, south-eastern China. Nest surveys were conducted from March to August in 2007 and 2008. The study site represents the highest peak of Wuyishan Cordillera, at an elevation of 2,158 m, with a mean daily temperature of 14.3°C during May and August, and mean annual precipitation of 1,500 mm. From June to August, rainstorms become more severe and weather conditions are extremely poor when typhoons occur.

Nest surveys

The 3-ha study area is predominately subalpine meadow habitat in which are situated more than 30 abandoned buildings and garages that provide suitable nesting substrate for the breeding martins. The nest of Asian House Martin is a closed cup typical of hirundines, built with tiny mud pellets and then lined with dried moss, 'sear' grasses and feathers, leaving only a small entrance hole. We classified two different nest locations: (a) under the eaves outside the buildings, or (b) inside the buildings. Where possible for each nest we recorded the overall size (width × height × depth) and the dimensions of the nest entrance (widest × smallest diameter).

Systematic surveys of nests and their contents began on 1 March in each year. Weekly visits were made to determine the arrival dates and record pre-breeding behaviour. Mist-nets (6–8 m long, with 1 × 1 cm mesh) were set 1.8 m from the ground to capture adult birds. For each individual caught we measured mass (g), total body length, wing length, tail length, bill length and tarsus length (all in mm). We banded the birds with coloured plastic rings and also marked each bird (using indelible markers) with a unique pattern on the throat and undertail-coverts to enable individual identification from a distance using binoculars following Massoni *et al.* (2007).

Once nest-building commenced, we recorded details daily. Four observers visited each nest every day to determine the exact timing of egg-laying. All eggs were numbered (in laying sequence) at the pointed end using a waterproof ink pen (Gosler *et al.* 2005). Egg length and width were measured to the nearest 0.01 mm using plastic vernier calipers, and egg mass was recorded to the nearest 0.1 g using an electronic balance. Egg volume was calculated as length × width² × 0.000507, following Manning (1979). Clutch volume was calculated as the sum of the volume of each egg laid in a clutch. Clutch size was defined as the number of eggs in the clutch at the onset of incubation.

Hatching date was defined as the date on which the majority of eggs in each clutch hatched. Synchronous hatching was defined as occurring when all eggs in the clutch hatched on the same day. Incubation duration was calculated as the time elapsed from the beginning of incubation to the hatching date. During the hatching period, nests were checked every day to monitor the incubation progress and obtain hatching dates. After hatching, we checked nests carefully every day to monitor the growth of nestlings and to determine the exact date they fledged. On each day, nestlings were marked with indelible markers on their legs, and weighed to the nearest 0.1 g with an electronic balance. The nestling daily mass gain and growth rate were calculated following Ricklefs (1968). Nestlings were not weighed after 18 days to reduce the possibility of premature fledging. Fledging date was defined as the date when

all nestlings left the nest, and the nestling period was calculated as the duration between the hatching and fledging dates. We determined the length of the breeding season for each year by calculating the number of days between the date when nest-building for the first breeding attempt commenced and the fledging date for the last clutch of the year.

Statistical analysis

Data were examined for normality using Kolmogorov-Smirnov tests, and we pooled the data of two years for subsequent statistical analysis. Comparison of breeding parameters across successive broods (clutch size, fledging morphology, number of nestlings, etc.) was conducted using non-parametric Mann-Whitney *U*-tests. Variation in the duration of incubation and other periods of the reproductive cycle across successive broods was examined using non-parametric Kruskal-Wallis tests. Spearman's rank correlation was used to detect the relationship between clutch size and the proportion of eggs hatching. Logistic regression was used to model nestling growth. Values are reported as means \pm SE with sample size (*n*) and range. Differences were considered significant at $P < 0.05$. Data were analysed using SPSS 16.0 (SPSS Inc. 2008).

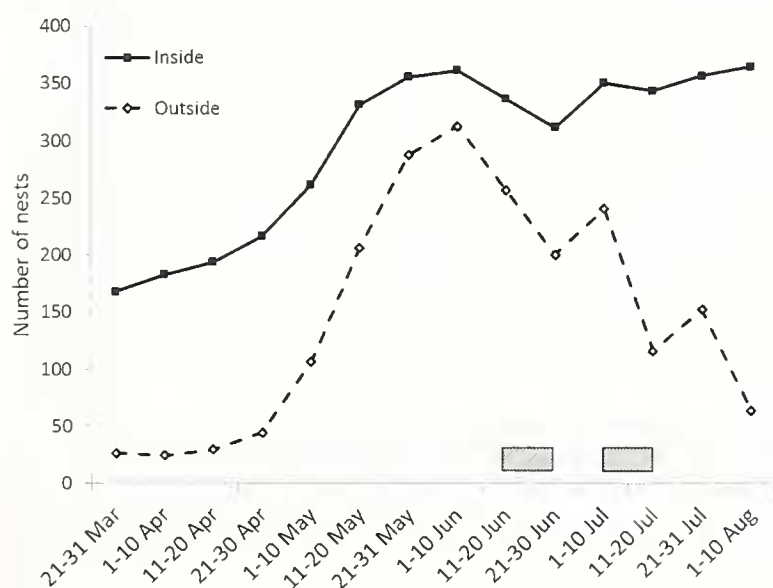
RESULTS

Nest construction and breeding

Asian House Martins were first observed in the study area on 13 March in 2007 and on 10 March in 2008, with nest-site selection and territorial defence by paired birds first observed in early April each year. Asian House Martins apparently preferred re-using existing nest sites: in 2008, all 195 nests remaining from the previous breeding season were re-occupied by the earliest-arriving individuals. Individuals that arrived later constructed new nests. The average external dimensions of nests ($n=37$) were 121.9 ± 4.5 mm (70–181.1 mm) wide, 109.3 ± 2.8 mm (73.9–130.9 mm) high, and 101.9 ± 2.6 mm (80–171 mm) deep. The average dimensions of entrance holes ($n=36$) was 37.3 ± 1.4 mm (18.3–60 mm) by 22.9 ± 0.6 mm (13.9–30.4 mm).

The maximum number of nests on any one day during the season was 628 in 2007 and 675 in 2008. The number of nests increased rapidly during April and May and peaked during June (Figure 1; results for 2007 were similar). The number situated outside buildings subsequently fluctuated and then declined after the end of August, whereas the number of nests situated inside buildings remained relatively stable (Figure 1).

Figure 1. Number of Asian House Martin nests located inside and outside buildings each month in 2008. Shaded blocks indicate the timing of severe weather events.



The first egg was laid on 20 April in 2007 and 27 April in 2008, when the majority of pairs had only just begun to construct nests. The last breeding attempt was recorded on 1 August in 2007 and 3 August in 2008. In both seasons, the Asian House Martin population had completely left the area by late August.

Clutch size, incubation, fledging and nesting success

Pooling both breeding seasons, we monitored 295 clutches totalling 834 eggs from 166 nests. Of these, it was possible to measure and collect data from 571 eggs. Clutch size ranged from 1 to 4 eggs (25, 52, 167 and 51 clutches contained 1, 2, 3 and 4 eggs, respectively), averaging 2.8 ± 0.1 eggs. No replacement eggs were laid if any eggs were lost. Eggs were coloured pinkish-white with blood-red spots just after being laid, but gradually faded to a pale white colour during incubation. On average, eggs were 17.9 ± 0.1 mm (15.5–21.3 mm, $n=558$) long, 12.9 ± 0.2 mm (11.6–14.6 mm, $n=558$) wide, and 1.5 ± 0.1 g (0.4–2.2 g, $n=571$) at laying. Mean egg volume was 1.5 ± 0.1 cm³ (1.2–2.2 cm³, $n=558$), and clutch volume averaged 4.2 ± 0.1 cm³ (1.3–6.8 cm³, $n=195$ clutches). Incubation by both parents (distinguished by colour rings) lasted 15.3 ± 0.2 days (7–25 days, $n=195$ clutches, excluding data from four nests with only one egg since we were unable to determine the exact date of incubation). There was no significant difference in the duration of incubation between clutches of different size (Kruskal-Wallis test, $n=191$, $\chi^2_2=5.46$, $P=0.07$).

The hatching proportion among all eggs in both two years was 0.66 ($n=834$ eggs). At least one nestling hatched in 75% (222) of all clutches recorded, and the mean proportion of eggs hatched in each clutch was 0.62 ± 0.02 ($n=295$ clutches); this was positively correlated with clutch size (Spearman $r=0.185$, $P=0.001$). Synchronous hatching was detected in 175 clutches (79%), asynchronous hatching in 47 clutches, with the majority of these (87%, $n=41$) hatching within 48 hours (1–5 days). The number of nestlings in a brood averaged 2.5 ± 0.1 (1–4, $n=222$ clutches). Among clutches which led to the fledging of at least one chick ($n=157$), the nestling period lasted on average 28.2 ± 0.2 days (22–35 days) and increased with the number of nestlings in a brood (Spearman $r=0.213$, $n=153$, $P=0.008$). For these 157 successful clutches, the mean number of fledglings was 2.5 ± 0.1 (1–4). The mean proportion of fledged nestlings in the clutches which had at least one nestling averaged 0.69 ± 0.03 . Of the 834 monitored eggs, 47% fledged. The mean proportion of fledglings per egg in a clutch was 0.44 ± 0.03 (0–1, $n=295$).

The survival rate (to fledging) of nestlings inside buildings was 0.84 ± 0.04 ($n=73$), which was significantly higher (Mann-Whitney *U* test, $n=166$, $P=0.006$) than the survival rate of nestlings outside (0.65 ± 0.04 , $n=93$). Severe weather conditions (rain and wind) caused by a typhoon in June 2008 resulted in the loss of 50 nests inside buildings and 112 nests outside. The total number of broods lost during two breeding seasons was 141 (48%, $n=295$). Of these, 72 were lost during incubation, comprising 46 (64%) lost owing to nest damage caused by severe weather conditions, and 26 (36%) owing to egg ejection by parental or other adult individuals for unknown reasons. During the nestling stage, 69 broods failed owing to severe weather (49 clutches, 71%), nestling starvation (10, 14%), eggs falling accidentally from the nest (9, 13%), and predation (presumed by a small rodent based on bite marks; 1 clutch, 1%).

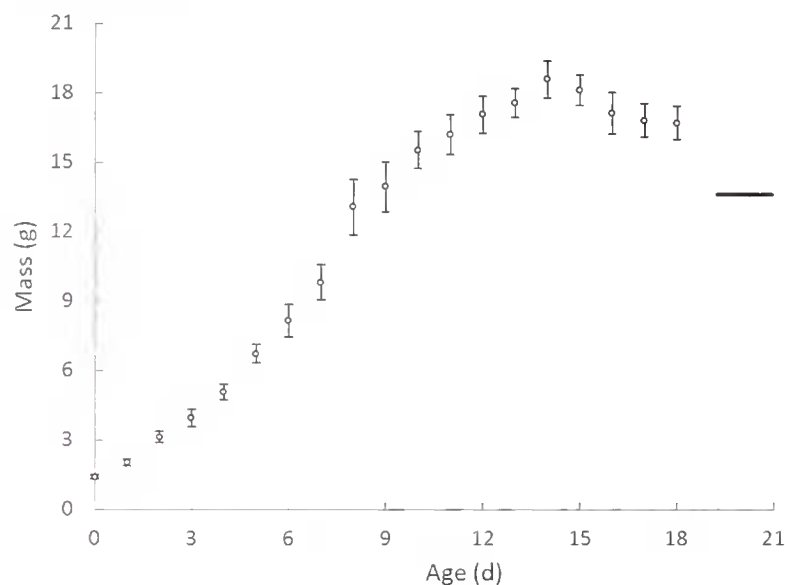
Nestling growth

We measured 381 individuals in 2007 and 2008 (199 adults and 182 fledglings; Table 1). There were significant differences between adults and fledglings in mass (Mann-Whitney *U* test, $n=333$, $P<0.0001$) and tarsus length (Mann-Whitney *U* test, $n=353$, $P=0.0001$) (Table 1). Mean mass of nestlings at hatching was 1.4

Table 1. Morphological characteristics of Asian House Martin adults and fledglings in study area (means \pm SE, with range in parentheses).

	Adult	Fledgling
Mass (g)**	13.5 \pm 0.1 (9.3–19.3) <i>n</i> =196	12.7 \pm 0.1 (11.1–15) <i>n</i> =137
Beak length (mm)	5.4 \pm 0.0 (3.9–7.7) <i>n</i> =199	5.5 \pm 0.0 (4.5–6.8) <i>n</i> =154
Tarsus length (mm)**	12.2 \pm 0.1 (9.3–15.9) <i>n</i> =199	10.9 \pm 0.1 (8.7–13.5) <i>n</i> =154
Wing length (mm)	93.4 \pm 0.2 (84.4–102) <i>n</i> =199	95.8 \pm 0.3 (57–111.5) <i>n</i> =172
Body length (mm)	111.6 \pm 0.4 (95.4–123.7) <i>n</i> =199	111.0 \pm 0.5 (100–128) <i>n</i> =133
Tail length (mm)	37.0 \pm 0.3 (26.4–47.2) <i>n</i> =199	37.4 \pm 0.3 (27.5–49) <i>n</i> =128

** Significant difference between adults and fledglings, Mann-Whitney *U* test.

Figure 2. Nestling mass (means \pm SE) as a function of age. Day 0 corresponds to the hatching day. The horizontal line indicates the mean adult mass.

\pm 0.1 g (1.2–1.5 g, *n*=5). Nestlings reached a peak mass of approximately 18.6 \pm 0.8 g at 14 days of age, but then showed a marked decrease to 16.7 \pm 0.7 g at 18 days (Figure 2). Fitting the mass as a function of nestling age to a logistic growth curve gave a growth rate constant (*K*) of 0.210.

Multiple clutches

After successful fledging of nestlings, a second breeding attempt was recorded for 79 nests (48%, *n*=166). The majority of breeding parameters from the second brood, in particular clutch size, hatching proportion, fledging success and nesting success, were significantly reduced when compared to the first successful

clutch (Table 2), except for the duration of both the incubation (Mann-Whitney *U* test, *n*=169, *P*=0.054) and nestling period (Mann-Whitney *U* test, *n*=136, *P*=0.93). Of the pairs that failed to rear their first clutch successfully, 39 also laid a replacement clutch. Of the 79 nests which had successfully fledged nestlings 44 clutches failed, for which 11 pairs laid further replacement clutches, but only three of these hatched nestlings and none fledged successfully. Replacement clutches for first broods also had significantly lower breeding parameters than the first breeding attempt (Table 2).

DISCUSSION

Our detailed description of the breeding parameters for Asian House Martins nesting at high elevation (2,158 m) reveals that they lay apparently smaller clutches (2.8 \pm 0.1 vs 3.4 eggs) but with larger eggs (1.5 \pm 0.1 vs 1.1 g) compared to colonies at lower elevations (data from Yu *et al.* 1998 and Mi *et al.* 2007, at 500 m and 1,290 m, respectively), presumably as a local adaptation to boost reproductive success by investing more in fewer offspring (Lu 2005), although we were unable to test this. The Jiangxi Wuyishan Nature Reserve breeding colony, with over 600 pairs, is the largest described to date. Typically, hirundines breed in smaller colonies (Snapp 1976), and smaller colonies of Asian House Martins are known at a number of lower-elevation sites (<1,800 m) in the Wuyishan mountains. The large colony size may be a consequence of a local shortage of nest sites (Snapp 1976, Shields & Crook 1987), but we were unable to test this.

We found that Asian House Martins at the Jiangxi Wuyishan Nature Reserve breed over a five-month period, from April until August, the beginning of which is apparently at least 30 days earlier than the equivalent date for a population at 1,290 m (Mi *et al.* 2007) and compared with Northern House Martins *D. urbicum* breeding at a latitude of 39°N (Saygili & Yiğit 2007). We speculate that this earlier initiation of breeding may be an adaptation to the increased risk of nest failure later in the season when extreme weather conditions are more likely.

Selection of nest sites offering greater protection from severe weather conditions was of critical importance to the breeding success in this population. We found that fewer pairs used more exposed nest sites outside buildings, and that such nests were subject to more pronounced fluctuations in nesting success than those located inside, owing to nest damage from heavy rain and strong winds. Such differences have not previously been recorded in hirundines, to our knowledge.

Asian House Martins produced multiple broods and replacement clutches in an attempt to maximise the number of

Table 2. Breeding parameters for successive clutches.

Breeding parameters	1st clutch	1st replacement clutch	2nd clutch	2nd replacement clutch
Clutch size ^{a,b}	3 \pm 0.1, 1–4, <i>n</i> =166	2.6 \pm 0.1, 1–4, <i>n</i> =39	2.6 \pm 0.1, 1–4, <i>n</i> =79	2.4 \pm 0.2, 1–3, <i>n</i> =11
Nestlings ^{a,b}	2.7 \pm 0.1, 1–4, <i>n</i> =136	2.2 \pm 0.2, 1–3, <i>n</i> =25	2.2 \pm 0.1, 1–4, <i>n</i> =58	1.7 \pm 0.3, 1–2, <i>n</i> =3
Fledglings ^{a,b}	2.6 \pm 0.01, 1–4, <i>n</i> =104	2.1 \pm 0.2, 1–3, <i>n</i> =18	2.3 \pm 0.1, 1–4, <i>n</i> =35	0, <i>n</i> =3
Hatching proportion ^{a,b}	0.7 \pm 0.0, 0–1, <i>n</i> =166	0.5 \pm 0.1, 0–1, <i>n</i> =39	0.6 \pm 0.1, 0–1, <i>n</i> =79	0.2 \pm 0.1, 0–1, <i>n</i> =11
Fledging success ^a	0.7 \pm 0.0, 0–1, <i>n</i> =136	0.7 \pm 0.1, 0–1, <i>n</i> =25	0.6 \pm 0.1, 0–1, <i>n</i> =58	0, <i>n</i> =3
Breeding success ^{a,b}	0.5 \pm 0.0, 0–1, <i>n</i> =166	0.4 \pm 0.1, 0–1, <i>n</i> =39	0.4 \pm 0.1, 0–1, <i>n</i> =79	0, <i>n</i> =11
Incubation period ^b	15.5 \pm 0.2, 7–21, <i>n</i> =111	14.7 \pm 0.4, 9–18, <i>n</i> =24	15.2 \pm 0.4, 10–25, <i>n</i> =58	15 \pm 0.6, 14–16, <i>n</i> =3
Nestling period ^b	28.4 \pm 0.3, 22–34, <i>n</i> =103	26.3 \pm 0.6, 22–30, <i>n</i> =17	28.7 \pm 0.4, 25–35, <i>n</i> =33	

^a = significant difference between first and second clutches (Mann-Whitney *U* test, *P*<0.05)

^b = significant difference between first and first replacement clutches (Mann-Whitney *U* test, *P*<0.05)

offspring they produce per season. However, mean clutch size, hatching proportion, fledgling success and nesting success declined significantly across successive broods. Declines in mean clutch size and hatching success through the breeding season have also been reported in other hirundine species (Zhao 1981, Sakraoui *et al.* 2005) and other migrant species (Dhondt *et al.* 2002). Multiple broods and replacement clutches have been reported for several hirundine species including Northern House Martin (Bryant 1979, Lahlah *et al.* 2006), Barn Swallow *Hirundo rustica* (Jones 1987, Sakraoui *et al.* 2005), Tree Swallow *Tachycineta bicolor* (Clapp 1997, Monroe *et al.* 2008), White-rumped Swallow *T. leucorhoa* (Massoni *et al.* 2007) and Purple Martin *Progne subis* (Allen & Nice 1952). In one experimental egg-removal study, 41% of female Tree Swallows laid replacement clutches (Rooneem & Robertson 1997), which is lower than the 63% of female Asian House Martins at the Jiangxi Wuyishan Nature Reserve. The capacity for laying multiple broods and replacement clutches has been shown in other species to be dependent on a number of factors including female age and quality, timing of first clutch, size of first clutch, and local resource abundance (De Laet & Dhondt 1989, Smith & Marquiss 1995, Tinbergen & Verhulst 2000).

Significant declines in breeding success across successive broods are often related to parental energy budgets and how many young both parents are able to feed (Lack 1968, Bryant & Westerterp 1980). Whether or not the declines observed for Asian House Martins are related to seasonal variation in prey abundance, or other environmental constraints imposed on the parents, remains to be seen. The seasonal declines in breeding success may simply reflect reduced foraging efficiency by parent birds caused by poorer weather during the later stages of the breeding season, as recorded in Barn Swallow (Pilastro & Magnani 1997), Tree Swallow (Nooker *et al.* 2005), Brown-chested Martin *P. tapeva* (Turner 1984) and Crag Martin *H. rupestris* (Acquarone *et al.* 2003).

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